THE UNPAIRED ECTODERMAL STRUCTURES OF THE ANTENNATA.

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A study of the Strepsiptera, and an attempt to relate their peculiar reproductive system to that of other insects, first suggested the homologies which it is the object of this paper to establish. The material was furnished by Prof. W. M. Wheeler, of the University of Chicago, to whom I am also indebted for much kindly help and valuable suggestion.

The unpaired median ectodermal structures of insects are of two kinds: (1) chitinous apodemes, or frucae, which occur in the thorax and serve for the attachment of muscles; (2) chitin-lined tubes or sacs, belonging to the various segments of the abdomen and forming the terminal, more or less differentiated portion of the genital ducts. A study of the occurrence of these structures throughout the Antennata, together with their embryonic development in a few forms, seems to indicate that they are homologous and derived from a series of segmental invaginations which were originally developed in relation to the appendages.

Considering first the apodemes: they are of very general occurrence throughout the insects, — we might even say the Arthropoda, — yet so far as I know little attention has been given to their structure and method of development. They usually consist of rod- or *T*-shaped inward projections from the intersegmental portion of the chitinous integument. Sometimes these projections are solid, but oftener they are hollow throughout their external third or fourth, thus giving evidence of their invaginate origin. The various parts may be bent or curved and give rise to minor projections, and their appearance may be further complicated by the union of successive apodemes. The free ends give attachment to muscles, and the intermediate part supports the connectives of the nerve chain.

The accompanying schematic figure after Graber will serve to give an idea of their usual form and function. x represents the apodeme in cross-section between two successive thoracic segments; m, points for the attachment of muscles; s, support for the nerve chain.

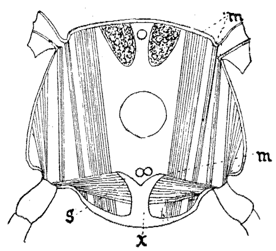

FIG. 1. — Transverse section through the thorax of an insect. (Schematic after Graber.) x., apodeme; m., points of attachment for muscles; s., support of nerve cord.

These structures reach their highest development and are most conspicuous where the power of flight is strongest, or locomotion is confined to only a few appendages. But we find a distinct beginning for them in the myriapods, where each body segment is provided with a pair of appendages. In *Scolopendra* (Fig. 3), for example, the intersegmental fold deepens toward the median line of the ventral body wall, and here we find attached two pairs of muscles. This intersegmental deepening is relatively uniform, with the exception of the first five segments of the body, where it is shallower to correspond with the slighter development of the legs.

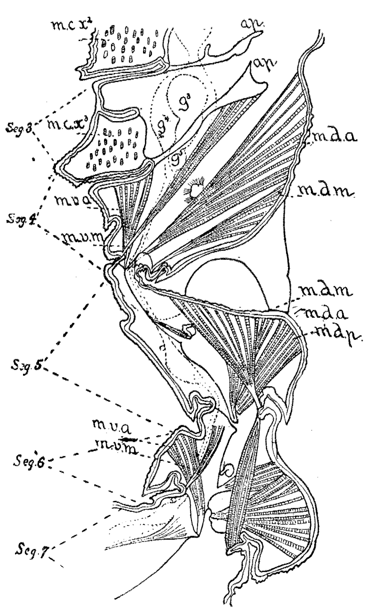

FIG. 2. — Sagittal section through *Myrmica rubra*. (After Janet.) *ap.*, apodemes; $g.^{3-5}$, ganglia; $m.c.x.^{2-3}$, muscles of coxae; *m.v.a.*, anterior ventro-lateral muscles; *m.v.m.*, longitudinal ventral muscle; *m.d.m.*, dorsal longitudinal muscle; *m.d.a.*, anterior dorsolateral muscle; *m.d.p.*, posterior dorsolateral muscle.

The accompanying figure of an ant, *Myrmica rubra*, shows the extent to which the development of the apodemes may be carried in a highly specialized insect. It represents a sagittal section through segments three to seven with the apodemes, to which the ventral longitudinal (*m.v.m.*) and the ventral lateral anterior muscles (*m.v.m.*) are attached. The dotted line represents the nerve cord.

Few observations have been made on the embryonic development of these structures. Ayers ('85), in his account of *Oecanthus niveus*, describes a median ingrowth between successive segments, which, as he states, atrophies late and "at the time of the closure of the dorsal wall of the body there is seen between the connecting cords of two adjacent pairs of ganglia a small triangular or cylindrical mass of cells, concerning the fate of which I am uncertain. I believe, however, they go to form a part of the internal skeleton. The chitinous rods in the thoracic region, to which the muscles of the legs and wings are attached, probably arise from the remnant of this median invagination, but in the abdominal region they may disappear entirely without giving rise to such structures." Wheeler ('93) describes and figures a similar series of invaginations in the *Xiphidium* embryo extending through the thoracic and abdominal regions, of which he says the former "are converted into the chitinous apodematous structures, which give attachment to some of the leg muscles." The latter disappear. This, of course, is just what we should expect if the abdominal ingrowth originally served the same purpose as the thoracic, but is now no longer functional. It is interesting to note, too, that in the embryos observed there occur evanescent traces of muscle-like cords running from the median ingrowth to the body wall (see figure).

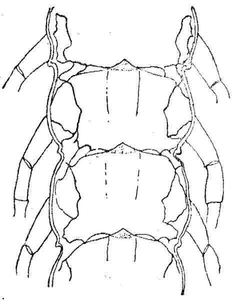

FIG. 3. — Two successive ventral segments of *Scolopendra*, seen from above, showing median deepening of the intersegmental depression.

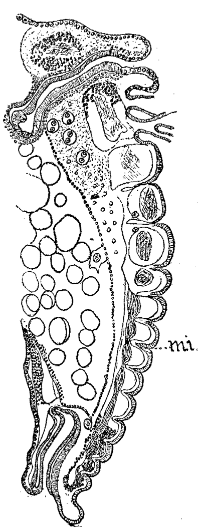

FIG. 4. — Median longitudinal section of embryo of *Oecanthus niveus*. (After Ayers.) *m.i.*, median invaginations.

Thus it appears that both comparative and embryological study indicate that the apodemes are parts of an originally metameric system of chitinous invaginations extending throughout the body and supporting the leg- and body-wall musculature.

Let us consider next the derivation of the terminal portion of the genital ducts. We rely here on some evidence of a more indirect character, but even then, it seems to me, the relations can hardly be questioned. In all the insect orders, with the exception of the male Ephemerids and some of the Dermaptera, the paired genital ducts open on the exterior through an unpaired terminal portion. This unpaired terminal portion arises independently from the integument, and during development comes into relation secondarily with the paired portion. It may be exceedingly slight in extent, as in the female Ephemerid, where it is merely a shallow depression between the seventh and eighth abdominal segments, the ovivalvula, as it is called, or it may be highly differentiated, as in the Dipteron, *Calliphora erythrocephala*, where, according to Brüel, it includes in the male the seminal vesicles and the ductus ejaculatorius, and in the female the uterus, vagina, and vulva. Palmén ('84), in a series of sketches, has shown the varying limit between the parts of mesodermal and of ectodermal origin. These figures have been so extensively copied in text-books that I deem it hardly necessary to reproduce them here.

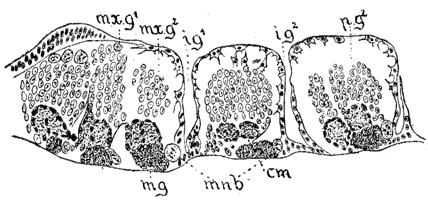

FIG. 5. — Sagittal section of the nerve cord of *Xiphidium ensiferum* a little to one side of median line. (After Wheeler.) *i.g.1*, *i.g.2*, first and second interganglionic depressions; *m.n.b.*, median cord neuroblasts; *m.x.g.1*, first maxillary ganglion; *m.x.g.2*, second maxillary ganglion; *c.m.*, median cord. (?)

The position of the external genital openings is very various. In Chilopoda it is terminal in the last segment. In the female *Pauropus* it is near the posterior border of the second postcephalic segment; the male apertures are paired, and the reproductive organs are otherwise so aberrant as to be hardly available for purposes of comparison. In most Hexapods the male aperture is between the ninth and tenth, the female between the eighth and ninth abdominal segments. In the Ephemeridea and some Orthoptera (*Blatta* and *Xiphidium*) the female opening lies behind the seventh segment. This instability in the position of the reproductive openings has been used

as evidence of origin from the homodynamous pairs of a series of metameric Nephridia and it seems to me that the argument might be similarly employed to account for the ectodermal portion of the sexual apparatus. Is it not probable that a primarily segmental Anlage made these conditions possible?

The condition of the Strepsiptera in this connection is most interesting. Here only the male undergoes complete metamorphosis. The female becomes sexually mature in the larval condition, and the young which develop from the egg in the body of the mother emerge through four median unpaired funnels, which open eventually near the posterior border of the second to the fifth abdominal segments, respectively. These funnels are curved toward the anterior part of the body and lined with chitin which is provided with outwardly directed spinules. Their general appearance reminds one strongly of the apodemes in some insects.

In the male there is a single genital aperture in the posterior border of the antepenultimate segment at the end of an unpaired chitin-lined ductus ejaculatorius. In both sexes the chitinous portions arise as unpaired ectodermal invaginations. The drawings give an idea of the conditions as figured by Nassanow ('**92**) for *Xenos Rossii.* My own study of the American *Xenos Peckii* gives identical results. Fig. 6 represents the three posterior segments of the adult male seen from above. *d.e.* is the ductus ejaculatorius; *v.d.*, the vas deferens; *t.*, testes; *m.*, muscles; *d.t.*, digestive tracts, with *c.*, coeca.

Fig. 7 is a sagittal section through a sexually mature female: *m.*, representing the mouth; *b.c.*, the brood canal; *b.f.*, brood funnels; *o.*, ova; *s.g.*, supra-oesophageal ganglion; *s.g.*, sub-oesophageal ganglion; *f.b.*, fat-body. Fig. 8 represents five stages in the development of a segmental brood funnel of the female, in which *e.* is used to designate ectoderm and *m.* mesoderm. Stage *D* persists during the development of the young, when the end of the funnel breaks through, giving place to Stage *E.*

The occurrence of funnels in four successive segments recalls the condition described by Heymons ('**91**) for *Blatta*, and Wheeler ('**93**) for *Xiphidium*, where the beginnings of the reproductive

system are segmental in the first to the sixth, and the second to the seventh segments, the metameric genital strand thus produced subsequently contracting and moving back to occupy

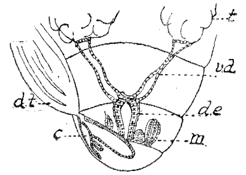

FIG. 6.

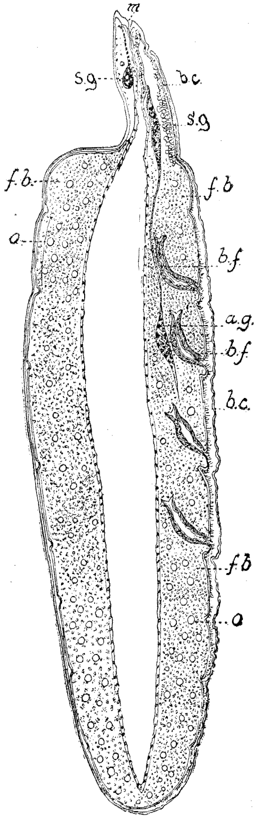

FIG. 7.

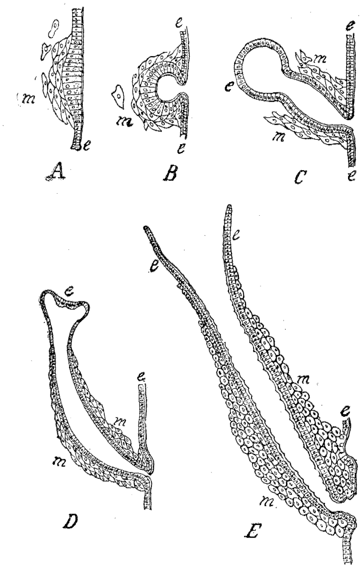

FIG. 8.

FIG. 6. — Three posterior segments of male *Xenos Rossii*, seen from above. (After Nassanow.) *d.e.*, ductus ejaculatorius; *v.d.*, vas deferens; *t.*, testes; *d.t.*, digestive tract; *c.*, coeca.

FIG. 7. — Sagittal section of female of *Xenos Rossii*. (After Nassanow.) *m.*, mouth; *b.c.*, brood canal; *b.f.*, brood funnels; *o.*, ova; *f.b.*, fat-body; *s.g.*, supra-oesophageal ganglion; *s.g.*, sub-oesophageal ganglion; *a.g.*, abdominal ganglion.

FIG. 8. — Five stages in the development of a segmental brood funnel. (After Nassanow.) *e.*, ectoderm; *m.*, mesoderm.

its usual position in the posterior part of the abdomen. The sexual organs are thus traceable to a primitive segmental type. Similarly the condition in *Xenos* may be regarded as the retention of a primitive character, as might be expected in a degen-

erate group such as the Strepsiptera. The primarily segmental Anlage, which made possible the varying conditions in the genital aperture, persists here in the development of ectodermal structures in four segments instead of only one.

The embryonic development throws further light on the origin of these structures. The conditions in *Xiphidium* and *Oecanthus* have already been described and figured. In the paper cited the abdominal invaginations are said to disappear, together with the rudiments of the abdominal appendages. And in a *Xiphidium* larva 3.5 mm. long the invaginations are seen for the most part to have grown much shallower, but the one lying just behind the ninth segment has grown only a little shallower and much broader, and has come to lie in close relation to the terminal ampullae of the genital ducts. This, then, is the pocket-like invagination, which later breaks through into the mesodermal ducts and becomes the ductus ejaculatorius. And we have here apparently the direct passing over of one of the segmental invaginations into the terminal ectodermal portion of the reproductive system.

We have, therefore, traced both the apodemes and the ectodermal part of the sexual ducts to a primitive condition, which is a mere median deepening of the intersegmental fold, arising in connection with the segmental appendages. This segmental arrangement of median ingrowths and appendages for all the body segments often occurs in the embryonic development of the higher Antennata, but the ingrowths for the most part disappear along with the ephemeral appendages. Only in the thorax, and here and there in the abdomen, they persist, become filled or lined with chitin, and, being brought into relation with the muscular or the reproductive system, serve as the apodemes or as the terminal ectodermal portions of the reproductive ducts in both sexes.

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